

1. On the Growth-forms and supposed Species in Corals.

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[Received June 15, 1907.]

(Plates XXVII.-XXIX.* and Text-figures 145-161.)

Before anyone engaged in the study of living creatures attempts to classify or arrange his material, it is essential that he should first observe, to the best of his ability, the life-processes of those creatures the affinities of which he would determine.

The zoology that deals with living animals must handle its material for study as living entities, it must observe the animals in their natural surroundings, must see the widest possible extent of their variation, and mark every influence of changing environment on the creature, before a cataloguing or an ordering of genera and species is undertaken. There should be no studying of living animals from fragments, as though they were creatures long since extinct.

I think it is true to say, that of all classes of animals the corals have suffered most injustice at the hands of zoologists, by reason of their being studied as fragments, and far from the site of their natural environment. It is also true to say that the collecting and describing of fragments of the vegetative growths of corals can lead only to confusion, for the conditions of the environment that produced the special characters of the fragment must always be carefully inquired into.

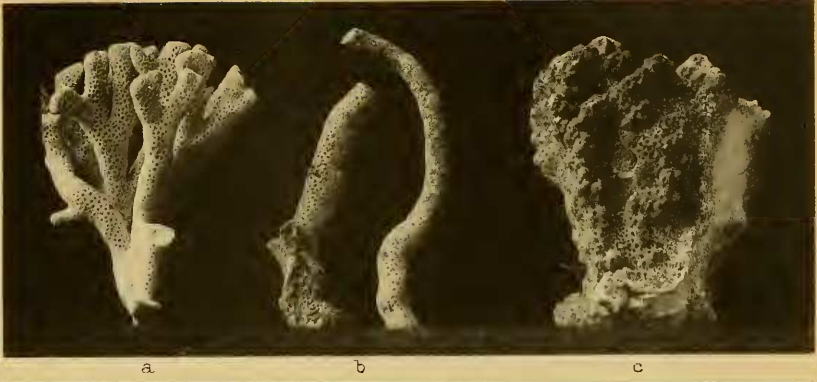
The corals constitute a chaotic collection of individuals, and the uncertainty as to what may be considered as a species is the first problem that must confront anyone who happens to study corals from his own resources on an isolated coral-reef. A gradually acquired familiarity with the actively growing corals in their natural habitat produces a gradual change in the standpoint from which a student would regard the limits of specific range; and a regular transition of ideas is undergone, from an early stage in which the number of species is believed to be limitless, to a final stage when the enormous variation in response to environment is recognised, and the actual species are known to be but few.

I am convinced that the only real advance that is likely to be made in the knowledge of a class of animals such as the reef-corals, must be the outcome of actual observation on the living colony; and the entire aim of my fifteen months' residence on the Cocos-Keeling atoll was the watching of the coral-growths in the endless variations of their natural environment.

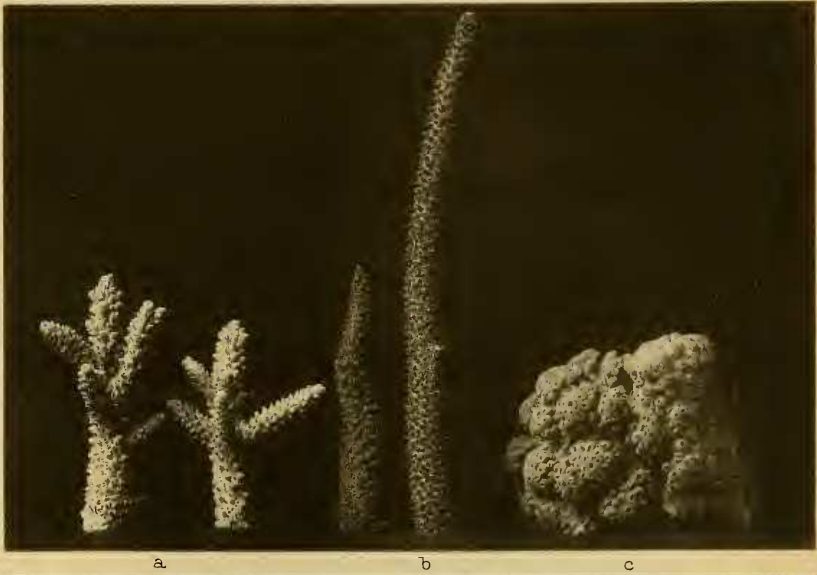
I would urge that if these observations have but little scientific value, yet they have this merit, that anyone without special knowledge, but with a love of Nature, may extend and repeat them; and I believe that along these lines lies the interest of corals.

* For explanation of the Plates, see p. 556.

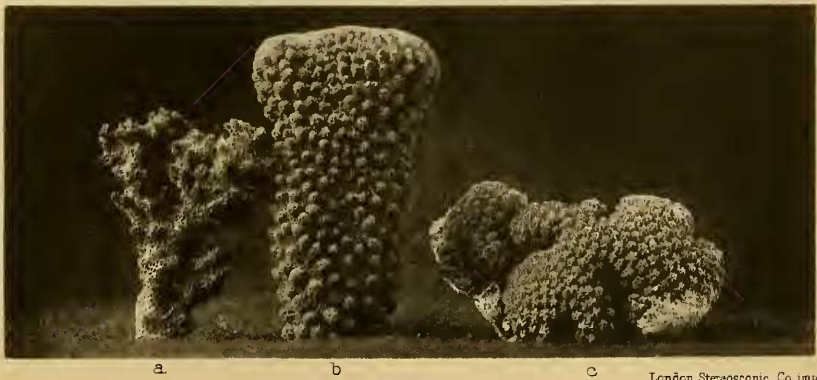
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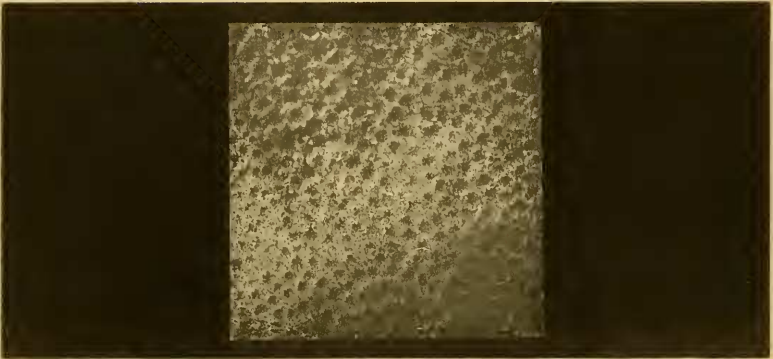


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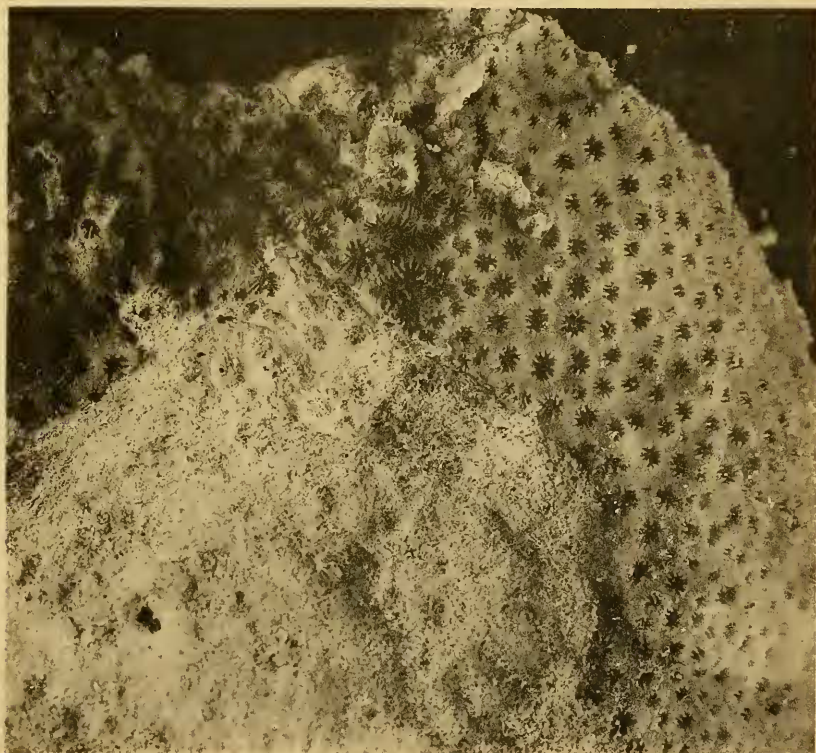
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INFLUENCE OF ENVIRONMENT ON CORALS.

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REPAIR AND DEATH IN CORALS.

The modern literature of corals and the modern methods of their study are devoid of interest, except to the museum specialist; and of those people whose lot is cast in places where excellent opportunities of study are at hand, many are prevented from making useful observations, by the wonderful maze of man-made difficulties that surrounds the study of a class of really interesting animals.

So as to introduce some order into the arrangement of the material collected and observed in the Cocos-Keeling group, it will be best to follow the life of the growing coral in its natural surroundings. The early stages need be touched on but lightly, and for all practical purposes the life of the colony may be considered to start with the fixation of the young larva. It is well known that the hollow, and as yet entirely uncalcified larva is expelled from the central cavity of the brooding parent, and in company with many hundreds of its kind is shot out into the water to take its chances of the tides and currents. It will at once be seen how varied may be the fortunes of the young coral, and how each individual embryo, endowed with its inherent growth-tendency, has a wide range of chance resting-places, that may happen to be suitable or not.

Every coral embryo launched into the world must start its career by becoming fixed to some nucleus, upon which it may build its future colony; and the nature of the nucleus, and its situation, though necessarily the outcome of the merest chance, are the determining factors in shaping the after destinies of the colony.

Coral embryos will become attached to almost anything in the water; they become fixed to older colonies, to shells, to dead coral masses, or even to floating pieces of wood; their resting place may chance to be of almost any shape, and to be situated in almost any environment. Now when the young coral starts its division, both the shape and the site of the nucleus are capable of modifying its method of division.

The asexual reproduction of corals is carried out by the division of the parent zooid, and the various methods by which this division is effected differ from each other considerably; and it is necessary to touch briefly upon the chief methods by which a zooid reproduces itself.

It is as well to state at the outset, and thus avoid much further explanation, that the different methods of division, though highly characteristic of certain well-marked types of growth, are not definitely and unalterably fixed; and I think it is justifiable to dogmatise, and state that *any form of coral may exhibit any form of division*. Since the resulting form of vegetative growth is purely the outcome of the type of division adopted by the zooid, then it follows that coral colonies may grow in many vegetative forms; and, again, these vegetative forms are not definitely fixed, for as any form of coral may exhibit any form of division, it follows that any form of coral may also exhibit any form of vegetative growth.

Speaking quite broadly, a colony may grow according to five different types of vegetative growth. It may grow as (1) a spherical mass, (2) an encrusting layer, (3) a free plate, (4) a branching tree-like growth, or (5) a mere amorphous lump; and though a definite inherent growth tendency is strongly implanted in the embryo, still the demands of the environment may call forth any type of vegetative growth.

The growth-forms are purely the results of repeated divisions of the zooids, and so it will be seen that the relative value, from a reproductive point of view, of the zooids in a colony, is a thing of the greatest importance. This consideration brings in its train the division of all the colonial corals into two groups of normal growth-forms; for all the zooids may take an equal share in the asexual reproduction, or again, some may be of greater importance than others, and the asexual reproductive functions may be lodged in a very few individuals only. These two great divisions must be considered separately, for the rules that may be applied to their respective methods of growth are widely different.

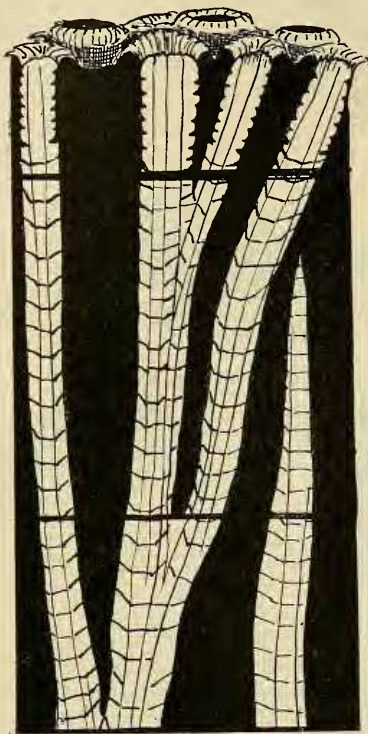
Taking first the class in which every unit is of equal value, and going back to the earliest origin of the colony, it is easily seen that a zooid "A" settled on a nucleus will divide into zooids "B" and "C," and "B" will further divide into "D" and "E," and "C" into "F" and "G," and so on; each newly-divided individual taking its equal share in future divisions. The natural outcome of this state of things is that, if the site of election of growth be a prominence, or, as is not uncommon, a small isolated fragment, then the equal divisions will tend to form a spherical mass. The rapidly growing colony will tend to surround the nucleus on all sides, and in this manner are formed those rounded masses of *Porites* and *Astræopora* that are commonly to be found lying free in sandy pools, and which, when broken across, are seen to be formed around a central nucleus, that generally consists of a fragment of dead and altered coral.

It is of course but natural that the true spherical form cannot long survive in very large colonies, for the zooids growing below are of necessity killed by pressure. The mass will therefore become a hemisphere, and continue its growth as a rounded boulder. This boulder-form is a very common type of vegetative growth among the reef-building corals; for if the growth starts as a perfect sphere, it will ultimately assume this form, and if the colony starts its growth on a basis that is not an isolated fragment, it will start this mode of growth from its first beginning.

There are many different ways in which the asexual reproduction of the zooids is carried out, for the budding and division may proceed in various fashions. The principal types of budding vary from each other in the actual site of origin of the daughter zooid from the parent, and in the degree of the final separation of the two zooids. These types, I think, do not merit individual description here, for what was said previously is true for them all,

and each, though highly characteristic as an inherent growth-form for a certain coral, may be assumed by many other corals.

Text-fig. 145.



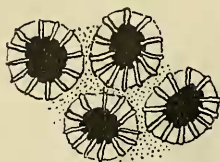
Vegetative reproduction in Corals.

Diagram to illustrate reproduction by equal budding: the transverse lines show the surface-level at the time when division took place.

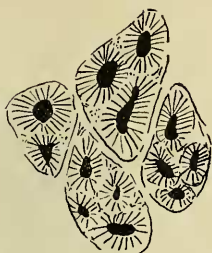
One method of division that is important among corals with zooids of equal reproductive value, is the type characteristic of the Meandrinæ (text-figs. 149, 150). In these corals the complete separation of the divided zooids is never carried out by the calcareous partition-walls, and so a more or less linear series of zooid mouths is formed. Tentacles fringe the margins of this series, and the resulting skeleton exhibits those well-known fissure-like markings that have given museum specimens the name of "brain-corals."

Now even such a highly characteristic type of division as that of the Meandrinæ may be assumed by other corals; and as sports,

Text-fig. 146.



Text-fig. 147.



Vegetative reproduction in Corals.

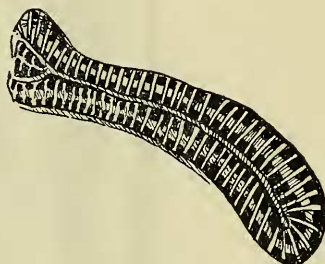
Text-fig. 146.—Type in which the daughter zooids become completely separated.

Text-fig. 147.—Type in which separation of the daughter zooids is less complete.

Text-fig. 148.



Text-fig. 149.



Vegetative reproduction in Corals.

Text-fig. 148.—Further stage of incomplete separation of zooids.

Text-fig. 149.—Meandrine type of division.

Text-fig. 150.



Vegetative reproduction in Corals.

Meandrine type of division : no separation of daughter zooids.

or even as localised patches in otherwise normal colonies, other corals may divide actively and yet form no calcareous partition-walls.

The meaning of these assumptions of an entirely foreign method of division is somewhat difficult to understand, but when an *Astrea* exhibits Meandrine fission, it is usually a sign that the colony is not flourishing and is in an unsuitable site; it would almost appear that the building of unnecessary partition-walls was too great an effort for the unhealthy zooids (text-fig. 151 and Pl. XXIX. fig. 2).

Text-fig. 151.



Vegetative reproduction in Corals.

Diagram showing an *Astrea* assuming (as a sport) a Meandrine form of division. From an actual specimen.

Again, the thickness of the intervening partition between two adjacent zooids is subject to endless variation, and in consequence the surface-pattern and the density of the coral may vary widely within the limits of a species. The same variation is to be seen in the level of the site of origin of the lateral buds, and this will have to be referred to later on, when the cause of the variations is considered.

Another feature that is subject to an excess of variation, and must therefore be considered, is the amount of raising from the general surface of each individual corallite. Every corallite of the colony may be flush with the general surface, or it may be raised from it in varying degrees, and the degree of raising gives very characteristic appearances to the colonies. The degree of elevation of the corallite is no safe criterion for determining specific rank, for it is a variable factor depending altogether on the reactions of the coral to its environment. The portions of the coral body that lie between the actual corallites are also important in this connection, for many characters that may have undue importance attached to them are displayed here. The interspaces may be smooth or rough, they may be sculptured in various fashions, and they may be elevated or depressed; but very great caution, and a very long study of the possibilities of variation, must be used by anyone who would assign specific rank to any of their forms.

Although a very large number of corals have the normal habit of reproducing equally from all parts of their surface, still evidences

may be seen, at many points of most colonies, that certain groups of zooids are more active than their fellows.

The special activity of these zooids may be due to purely local causes; it may be called forth merely by irritation of a localised portion of the surface of the colony; or it may be a real alteration of vegetative habit. It is an outstanding fact about all the colonies observed for long intervals, that the growth tends to become irregular—at different times different portions of the colony have sudden phases of active growth, and these may be due to no observable cause. Again, some zooids of the colony may have special advantages due to the environment, and these zooids will grow and divide excessively, in such a manner that they dominate the growth of the whole colony, and consequently modify its form. The conditions of the environment may call forth special reproductive activity in any portion of the growth, and so in a colony, all of whose units are of equal importance, some part will be found to be growing onwards, whilst all the remainder of the zooids are practically at rest. In this way the typical hemisphere of such colonies may become modified as a creeping plate, an encrusting layer, a pseudo-branching form, or a mass of mere irregular nodules.

In those corals whose zooids are naturally of equal reproductive importance therefore, forms may arise, from physiological need, that simulate exactly those forms whose zooids are naturally of differing reproductive value.

Turning now to the corals that constitute the second class, and have some of their units specialised as active agents of growth, it is at once seen that the possibilities of variation of normal vegetative habit are greatly increased. All the elaborate branching forms, plates, and leaf-like growths belong to this class; and all are evolved by special peculiarities of the growing point. The zooids that constitute the growing point may take various forms: they may be arranged as a cluster, as a creeping edge, or as many varieties of terminal shoots of branches.

In the first instance, it is necessary to draw very sharp distinctions between two subdivisions of this group. In *Group 1* come all those forms like *Montipora*, whose distal zooids are the newest formed members of the colony (text-fig. 152); and in *Group 2* are included the Madrepores, whose distal zooid is the most ancient individual in the whole growth (text-fig. 153, p. 527).

In dealing with *Group 1* many forms have to be considered, for when the youngest are the active cells their growth-cluster may be very variously disposed, and on its disposition the resulting vegetative form entirely depends.

When the growing cells are arranged in linear series, a flat growth will result, which grows from one of its edges, or from them all; and in this way an encrusting layer or a free plate may be formed. Corals that grow with a linear growing point may settle down on a basis, and spread over it in all directions, taking

an exact impression of every irregularity of its contour; and then, reaching the limits of the basis, they may grow from it as flat plates, spreading out from its margins. Such corals as grow in this fashion show many curious changes at their free margins, for although the superior surface of the encrusting layer can alone produce zooids, still at the free edge zooids will appear on both superior and inferior surfaces.

In connection with these partial plates a very curious fact is always demonstrated, for the whole surface structure of the coral body, and of the corallites, differs above and below; and this important fact will need further reference. A coral may start from its first beginning by growing as free exfoliating plates, and then it may bear zooids on both surfaces of the plates, or on the upper surface alone. In every case where zooids are borne both above and below, there is the same marked difference of structure between the two surfaces.

Text-fig. 152.



Vegetative reproduction in Corals.

Diagrammatic section to illustrate the mode of growth of Montipores:
the uppermost zooids are the most newly formed.

When the linear growing point grows uniformly upwards, the resulting growth consists of a series of vertical plates; and when the growth takes this form, the structure of both sides of the plate is identical, and zooids grow from both surfaces.

A plate-like growth is formed by a uniform and continuous growing edge; but the linear series of young growing cells may not maintain their continuity: the growing edge may reach a certain size and then divide, and the resulting growth consequently takes the form of a plate, cleft at its edges, or of a branching form, all of whose branches are given off in one plane. This is a highly characteristic form of growth of one type of Montipore

that is abundant in the islands, and it grades very naturally into the plate-like growths on the one hand, and into the complicated branching forms on the other.

In the many highly branched forms of vegetative growth, the growing cells form a cluster, and this cluster divides as it grows upwards, with the development of many growing points at intervals on the parent stem. The cluster may be of various shapes, and its form determines that of the stem that results from it. The stem may be rounded or flattened, may be thin or thick, and it may branch at frequent intervals, or it may scarcely branch at all, so that straight rods of uniform thickness may be characteristic of the vegetative growth of the coral.

Another modification of this method of growth is that in which practically the whole colony represents the growing point, and then the entire mass grows upwards as a solid column; or the growing point may be confused and irregularly distributed, and then an irregular, lumpy amorphous mass results.

Whatever the vegetative growth may be, it is in these cases the product of a mass of growing cells, and these cells are being perpetually renewed, so that the growing point always contains the youngest cells in the colony.

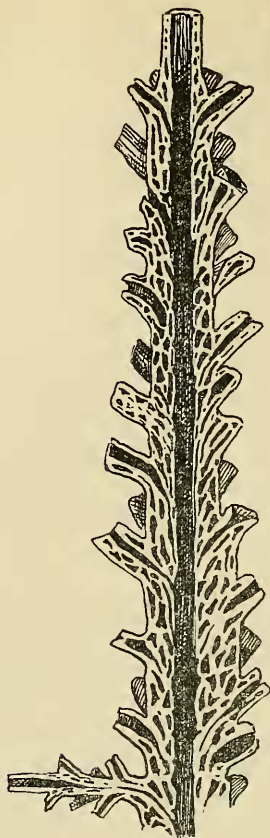
In *Group 2*, however, this state of things is entirely altered, for there one zooid, which is situated at the extremity of the stem, and which I shall call throughout the "dominant apical zooid," constitutes the growing point; and this zooid is the parent of the entire colony.

The zooid that settles down to establish a Madrepore colony has the peculiar innate property of perpetual growth and perpetual youth; and this original zooid grows up and up, budding new zooids from its sides, until destruction overtakes it. As a matter of fact, a Madrepore colony usually starts as a flat growth which spreads from its edges, but this method of growth lasts for only a very short time; and all the characteristics of the "dominant zooid"—which is here the central zooid—are even then well marked.

Besides possessing these peculiar physiological distinctions, the "dominant zooid" is marked off from its fellows by a great anatomical feature, for it is a symmetrical zooid. Of the many thousands of daughter zooids budded off from the "dominant zooid," all are not alike; the great bulk are asymmetrical, and are but little raised from the general surface of the coral, but here and there a prominent and symmetrical zooid is given off. Like the "dominant zooid," these lateral zooids possess the power of perpetual growth, and they are the agents in forming the lateral branches. Under certain conditions only very few of these prominent lateral zooids are produced, and then the resulting vegetative growth consists of long straight stems with but few side-branches.

The typical form of vegetative growth of the Madrepores is therefore a branching system, but many variants of this form are

Text-fig. 153.



Vegetative reproduction in Corals.

Diagrammatic section to illustrate the mode of growth of Madrepores :
the "dominant apical zooid" is the oldest member.

developed normally and abnormally. Pseudo plate-like growths are common, and they are formed by the anastomosis of numerous branches in one plane. Again, the importance of the "dominant apical zooid" is variable, and some types branch more after the type fashion of the Montipores, for a whole apical series of zooids may be symmetrical.

Having now reviewed, in some measure, the various methods of the formation of the vegetative growth of colonies, it is necessary to see how far these forms of growth are to be reckoned as specific qualities. Here a great difficulty arises, for an enormous amount

of time and careful experiment must be devoted to the proving or disproving of each individual case; and though, after long familiarity with living corals, one may feel certain that two entirely different vegetative forms belong to the same species, yet the conclusive proof may be lacking.

Collecting very extensive series of variations will, in some cases no doubt, link up extremely diverse forms, and the studying of the repair of damaged specimens will serve to make clear others; but experimental breeding, and the rearing of identical species in diverse surroundings, must be the final test in most cases. Now this is a work of extreme difficulty, for an adult colony, when removed from its own environment and placed in a different one, almost invariably dies, and the artificial rearing of corals is very troublesome; my experience of corals in aquaria is that it is very difficult even to keep them alive.

The only method that is open to every resident in places where corals flourish, and the one that I followed in the Cocos-Keeling atoll, is the careful noting of every modification of colonies the life-surroundings of which differ by reason of some influence that can be easily recognised. By this I mean that the corals of deep water and shallow water should be compared; those living in the surf and those living in calm spots should be noted; and the corals living exposed to sediment should be contrasted with those living where no sediment is being deposited.

These are extremes of habitat, and at first the corals of two entirely different environments will seem to be quite distinct, but every compromise of conditions will be found in different spots in an atoll, and with every grade of altered surroundings it will soon be seen that there is a modification of coral-growth; and the more completely this method of observation is carried out, the more will the types of extremely different habitats be found to be linked up by intermediate forms. It will be best to study the influence of the different conditions of life-surroundings on the form of vegetative growth, by taking the different possible modifications of environment in order; but first some general growth tendencies of all corals must be made clear.

As a rule, coral zooids and coral colonies tend to grow upwards, and the general form of vegetative growth depends on this fact.

To this rule there are two noteworthy exceptions in this atoll, and these corals (*Ctenopsammia willeyi* and *C. nigrescens*) generally grow with their zooid mouths turned downwards. Now I think these exceptions to be not without interest, for both these corals live in dark places,—they prefer in fact the under sides of boulders, and they possess no symbiotic algæ in their tissues. They are coloured respectively red and black; and I would put it forward as a speculative idea, that it is the innate tendency of the symbiotic algæ to grow upwards, rather than any innate property of the corals themselves, that causes the general growth tendency of the corals.

It is true that the zooids on the lower surfaces of plate-forms

grow downwards: but as a rule I believe those horizontal plates that bear zooids below are but variant forms of growth of other types: for such corals as have no growth-form except that of a flat horizontal plate do not as a rule bear zooids below.

Some further remarks must be made about plate-like growths; but here is a convenient place to refer to a rather strange fact that Darwin called attention to, and this is, that vertical plates grow so that they offer their flat surfaces to the currents. The same thing is true of growths that are branching forms, for then the plane of greatest branching is that at right angles to the line of current. At first sight this seems a strange thing, for plates growing in rough water become so much more exposed to damage; and yet it is doubtless for the exposure of a larger surface of zooids to the food-bringing currents, that the plate spreads in this direction. This phenomenon is especially notable in the Millepores, the broad laminae, or fan-shaped growths of which are always opposed to the line of the waves, even when the colony happens to dwell in very rough water.

Two general rules may therefore be laid down that apply to all the forms of growth that have been described: the first, that all corals having symbiotic algae tend to grow upwards; the second, that all tend to offer their greatest surfaces to the line of currents.

We may therefore assume that every coral embryo that settles upon a site of election, and starts the foundation of a colony, has three inherent tendencies: it has its inherited type form of vegetative growth, and its inclinations to grow upwards and to oppose its growth to currents. Now these tendencies are affected by the nature of the water in which the embryo settles down; and for nearly every coral there is a modification of vegetative growth dependent on the environment: thus most corals have a deep-water form, a smooth-water form, a rough-water form, and numerous variations depending upon the amount of sedimentation that is taking place in the water of their habitat. A coral that grows in rough water is obviously exposed to injury; and those people who have stated that the home of election of the corals is the surf-beaten edge of the barrier, have made an error of observation and of fact. The comparatively lifeless zone of a coral-reef is that part of the barrier that is exposed to the maximum force of the surf, with the rising and falling of the tide.

Such corals as do grow in the almost perpetual crash of the surf are of a very easily recognised type; and when contrasted with the forms of the same species that have lived in calmer waters, they appear to have very few points in common. The type of vegetative growth best suited to resist the force of the waves, is of course the rounded or flattened massive boulder; and the *Porites* masses are the type to which all such growths tend to conform (text-figs. 158, 159, pp. 540, 541).

This rounded form of growth is brought about in several different ways: in *Porites*, and other corals, where the equal

reproductive value of all zooids tends to the production of a sphere, it is of course the normal habit of growth; and so such corals have their natural home in the rougher water, and undergo their atypical modifications when developed in other sites.

All branching forms, when growing in rough water, are subjected to a change of habit of vegetative growth; and this change is a very interesting one. It will be pointed out when the process of repair is dealt with, that injury affects various forms of corals differently; and all these rough-water forms are in reality the result of perpetual injury.

It would be an obvious disadvantage to a coral to adopt a highly branching form, when living on the surf-beaten portion of the barrier; for the colony would soon be wrecked and broken up by the waves. There is no Montipore in the atoll that lives by election in rough water, but occasionally colonies become exposed to strong currents; and then the perpetual injury to the upper portions causes the growing clusters to be broken up and confused; and the resulting growth is an irregular mass of short stunted branchlets.

Montipores in rough water may also take on a creeping habit of growth, and form encrusting layers on the surface of dead massive colonies; but they are not corals that are at all common in any but the calmest water. Their usual home is the lagoon, and the greatest normal departure from their favourite habitat is in the current-swept shallow inlets to the lagoon; and here an endless series of modifications may be collected, ranging from branching forms to mere amorphous masses and encrusting layers. (Pl. XXVII. fig. 1 c.)

The rough-water forms of the Madreporae are highly characteristic, and all depend on the processes that always occur in this group when the "dominant apical zooid" is injured. Instead of a growth that consists of few dominant zooids situated at the extremities of long branches, a rounded mass is formed; and it is composed of little groups of symmetrical zooids surrounded by others that are asymmetrical—each little group representing a branch in an extremely abbreviated form.

From these extreme rounded masses, with branches that are mere bosses on the general surface, every transition form may be collected, up to the highly developed lagoon types, with branches many feet in length.

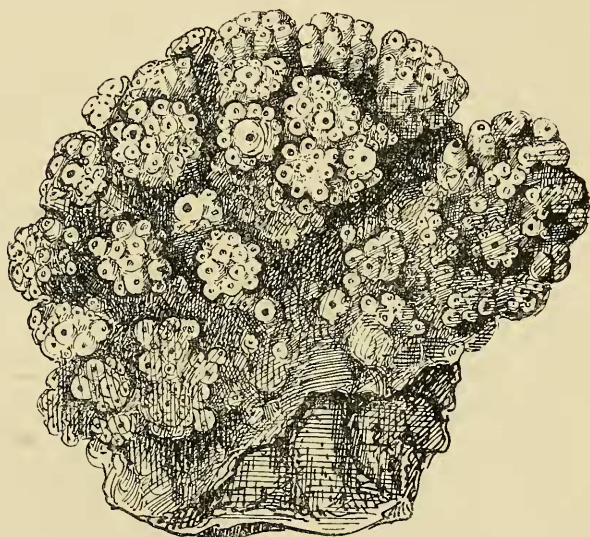
Exactly the same results are produced in the Pocilloporae, and here the rough-water type is a flattened growth, with irregular divisions into separate lobes; each lobe representing a separate branching system (Plate XXVII. fig. 3 c).

Any coral that chances to establish its colony in rough water exhibits therefore one well-marked characteristic: it always tends to form a rounded, or flattened mass; and this for obvious mechanical reasons. It is a direct outcome of the conditions of the environment, and any zooid must conform to it or perish. Repeated injury to the growing cells is the determining cause of

this method of growth; and though the fully developed colony is so totally different to the calm-water form, still the process is easily seen in the making by means of artificially inflicted injury.

Besides the alteration of the general appearance of the vegetative growth, the rough-water environment causes other changes in the coral; for it is diagnostic of a rough-water coral that its structure is compact and dense, and its corallites tend to be flush with the general surface of the growth. The question of the raising of the corallites will have to be discussed again when the action of sedimentation is gone into; it must be stated here, that though the levelling of the corallites in rough-water types is doubtless partly mechanical, it is also due to the fact that in rough water sediment does not tend to be deposited.

Text-fig. 154.



Rough-water type of highly branched Madrepore; from an actual specimen of *Madrepora pulchra* taken from the barrier.

In marked contrast to the rough-water types are those forms of a species that happen to have become fixed in an environment where the water is more or less calm; and here, as every grade of environment is to be found, every grade of modification of the colony is represented.

Corals grow in great luxuriance on the wave-stirred outer slopes of the atoll, but this is a site by no means to be confounded with the surf-line of the barrier. They grow also in the numerous pools of the barrier flats, in the inlets to the lagoon, and in the

lagoon itself; and each environment has its own peculiar conditions.

In the barrier pools every modification of life surroundings is to be met with, for these pools are of varied depth, they are filled with sand, or are of bare rock; and they have a varying exposure to the wave action of the barrier breakers. Corals grow luxuriantly in most of them, and they afford the best field for experimental work. Since their conditions change with every cycle of the tides, they form the meeting ground of nearly all the commoner species, for they afford in turn most phases of natural environment. Here are found the highly branched Madrepores and Pocillopores, and many Astreas. The colonies are distinguished as a rule by having their corallites raised, for in most pools sand is being deposited. They are also highly branched and of a bushy form, for they are exposed to injury by moving fragments, and so branch formation is stimulated, whilst the great development of individual branches is limited.

These rock-pool forms show naturally the graduating series of types that connects the rough-water forms and the smooth-water forms; and they show also the intermediate stages of the development of coral structures that are intended for the resistance of the action of sediment.

In the smooth-water forms, the predominant feature of the colony is the fragile nature of the growth. Contrasted with the rough-water forms, these colonies are extremely lightly calcified, and their branching systems are distinguished by their delicacy. Their branches are long and slender, their structure is far more porous, and their whole appearance is quite different to that of the colonies of the same species that chance to reside in wave-beaten areas. (Pl. XXVII. figs. 1 *a*, 2 *a*, & 3 *a*.)

The smooth-water forms lead the way to those growths of corals that inhabit the deeper pools of the lagoon. The deep-water forms are the most fragile of all: their growths are more attenuated, and their branches are given off at far less frequent intervals. There is practically no damage inflicted on the growing points—whether they be growing clusters, or “dominant apical zooids”—and so lateral branch formation is never stimulated. Several of the forms of *Montipora* and *Madrepora* that occur in from 8 to 12 fathoms in the lagoon, are mere cylindrical stems, of great length, and with practically no lateral branches whatever. (Pl. XXVII. figs. 1 *b*, 2 *b*, & 3 *b*.)

Besides the attenuated form and the absence of lateral branching, one other feature distinguishes the comparatively deep-water forms from those that inhabit the surface waters,—and this is the general absence of pigment throughout every portion of the colony. Deep-water forms are therefore as a rule pale or entirely colourless.

It will be seen from these instances that the form of the colony varies as the outcome of the influences of the environment; and every embryo that settles in any habitat has to comply with the

demands of the physical conditions, and modify its inherited growth tendency,—or perish. Totally different forms are produced in totally different environments, but these forms must not be regarded as “species,” for they are mere variations of vegetative growths in response to the necessities of the life surroundings of the colony.

The type of vegetative growth is affected mostly by the physical conditions of the water in which it lives, but the actual structure of the coral depends greatly upon the presence, or absence, of sediment. Some very strange results are produced by waters in which sediment is held suspended, and from which it is being deposited; and sediment will alter the appearance of a coral more strikingly than any other influence. The deposition of sediment is the greatest agent in causing coral death: corals are very easily killed by even comparatively little sediment, and are profoundly altered by it, if they are to successfully resist its influence.

The extent of silt formation at the surface of an atoll in mid-ocean is hard to imagine, and it has certainly not been appreciated by those experimenters who have attempted to estimate the age of an atoll by catching the silt in a net, as it passes into the lagoon. Adown the submarine slopes of the atoll, for a hundred miles east and west, the bottom was found by the cable soundings to be finely trituated coral-sand, and it is only an uncertain and inconstant fraction that passes into the lagoon. Silt is one of the shifting influences of the atoll, and so may visit the coral colonies for only a brief portion of their lives, and then partial death and strange repair-growths result. In the lagoon, and in some portions of the barrier pools, silt is a constant factor, and here shows to the greatest advantage the modifications that it is capable of producing in coral-growths. Speaking generally, silt alters the vegetative growth-form of colonies only in as far as it produces flat-topped rock masses by killing the uppermost zooids, and causes amorphous and irregular growths by partly killing the uppermost growing cells of the growing points. But in the surface structure of the coral, it produces great and wonderful changes. Its effects are best studied by comparing the upper and lower surfaces of partial plates. In these plates, the upper flat surface is alone exposed to the action of the deposition of sediment, and here the corallites tend to be small, and to be raised from the general surface, and the intervening spaces themselves tend to be sculptured and complicated in various ways (Pl. XXVIII. fig. 2). Below, the corallites are larger and are flush with the general surface, and the intervening spaces are flat and plain (Pl. XXVIII. fig. 1).

Now this condition is entirely the result of the attempt of the uppermost zooids to build a silt-resisting structure.

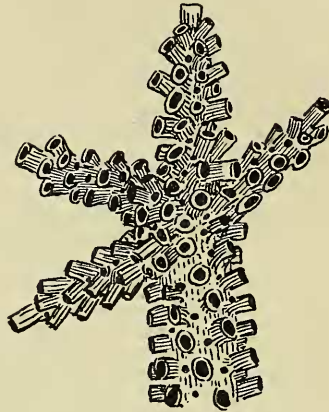
The corallites are smaller, and are raised from the general surface in order to minimise the chance of silt dropping in and choking the zooid. The intervening coral body is variously sculptured

and grooved for the carrying off of sediment, that happens to lodge upon the surface of the colony. Wonderful series of modifications are formed in this way; and a single species shows extreme variations in the size of its corallites, and in their raising from the general surface, when specimens collected from different habitats are compared.

Text-fig. 155.



Text-fig. 156.



Text-fig. 155.—Diagram of type of growth of a Madrepore when living in water free of sediment: *M. pulchra*.

Text-fig. 156.—Diagram of growth of *Madrepora pulchra* when living in a habitat exposed to the action of sediment.

The size of the corallite and its projection from the surface are therefore not safe specific features; for corals of identical species, from sediment-carrying water and from absolutely sediment-free water, exhibit great modifications of these characters.

The vegetative habit of a coral, as we have seen, is no true index of its species; and its method of asexual reproduction, the characters of its corallites and surface structure, and also its coloration, are equally variable.

Coloration depends on many, and very little understood, influences. Corals from deeper waters lose their pigment; and corals that are struggling hard in adverse circumstances—corals in fact that are often about to die—become highly pigmented.

Corals identical in every other respect, and living side by side, may be differently coloured; and nothing is more familiar than the purple, brown, yellow, or greenish *Porites* masses that live under exactly the same conditions, as far as can be determined. Even one colony may be differently coloured in different parts. In *Pocillopora* there is a dimorphism of coloration, some growths being pink and some pale brown: the pink is a very beautiful

and striking colour, and yet the corals are identical when dead, and the zooid in both cases is the same.

Montipores vary from yellow to olive-green and brown, and yet the zooid is always of the same sulphur-yellow, and the coral is always identical in other respects.

The general coloration of the coral body cannot therefore be regarded as specific, and the coloration of the zooids also shows a strange inconstancy. Although as a rule the zooids of different colonies of identical species—though the colonies may be very different in appearance—are similar, yet in one colony the individual zooids may be very variously coloured.

There is one very striking case, that is not uncommon in the atoll, of an *Astrea*, where the zooids on the upper surface are a fine fluorescent green, at the sides of the growth brown, and below white. And here it would appear—as also probably in the deeper water forms—that light had some influence on the production of the pigments. Despite this peculiar variation of the colour of the zooids in one colony, it remains a fact that the zooid is the true index of the species. In all the strange growth-forms and abnormal coloration of *Pocillopora* the zooid remains constantly brown; and in *Montipora*, constantly pale sulphur-yellow. In *Stylophora*, whether the coral is the thinly branched and colourless deep form, or the thickly branched and brownish shallow-water form, the zooid is always of the same yellow colour.

In considering the vegetative forms of the corals of an atoll, it must always be remembered that the environment is not a constant one. Although the coral colony is absolutely debarred from changing the site of its growth, still the physical conditions of its surroundings are always altering. The terms rough water and smooth water, deep or shallow, and sedimenting or non-sedimenting, are therefore only comparative; for what to-day is a habitat free from sediment, may in the course of a few weeks become the site of a copious deposition of silt. The rise and fall of the tide across the barrier must of necessity cause great changes in the life surroundings of the corals in its passage; and so a colony, found in a calm pool, may for a part of its life be exposed to violent wave action. This must always be borne in mind, for the results obtained by careful collecting will not be pure. Corals may be found of different forms, growing in close proximity; but far from being evidence that they are different species, and not mere varieties, they demonstrate the fact that the physical conditions of their surroundings are inconstant, and that, for a cycle each form is, in its turn, the most suitable.

The very inconstancy of the environment is one factor in showing the plasticity of the corals, for the partial death and repair caused by changed conditions afford striking evidence of the wonderful powers of varied building possessed by the zooids.

Experiment with constant physical surroundings must be the

ultimate test of variability, and in this connection a very interesting case may be quoted. In the lagoon, a large portion of a tree-trunk was floated, and made fast to an anchor and chain; the wood was used to float a ship's moorings, and remained just two years in the water. When it was removed in 1906, several colonies of *Pocillopora* had started growths upon it, and they had taken up different positions around its circumference. The colonies growing above were flattened bosses; those on the sloping sides showed more tendency to branch; and those below its convexity were delicate branched forms. (Pl. XXVIII, fig. 3.)

Now the environments of these colonies were very different, and they were absolutely constant; at all states of the tide, waves broke upon its upper surface, whilst the sides were in gently moving unbroken water, and the bottom was in comparative calm. The growths might be referred to many so-called species, and they represent many types found in the atoll, and yet no one may justly doubt that they are identical, and that their vegetative growth is entirely the outcome of their differing environment. I believe that this natural experiment indicates the lines along which the real understanding of the "species" of the corals is to be arrived at.

So much for a case in which the constantly different environment caused the production of different types, that would be incorrectly considered as different species; it is now best to follow those cases in which altered environment produces variation in the colony, and causes repair growths to assume entirely different forms to that of the original colony.

Although corals as adults do not have the power of independent motion, but must live and die in the spot where they originally settled down, still they have the characteristic that belongs primitively to all protoplasm—they are capable of resenting injury, and of moving their parts in response to stimuli. If, when in the course of a walk on the barrier, a mass of coral be found the zooids of which are actively extended, it is easily seen that a very slight stimulus will cause them all slowly, but very certainly to retract. A light brush of the surface or a gentle touch will cause a slow response, and the zooids withdraw themselves over the definite area affected. Of the solitary corals *Fungia* furnishes a good example of resentment of injury, for if a living specimen be touched, the delicate tissues covering the rays of its skeleton slowly shrink and become pale, and this condition spreads as a slow and curious wave. The sensitive tissue of the creature thins out over the exposed portions and retracts into the spaces between the rays, so that, from being a delicately glandular and prettily coloured mass of soft tissues, it becomes an almost colourless piece of stone.

These movements of parts are the animal's only means of

avoiding injury, and though they afford some protection to the more delicate parts of the zooid, a danger that threatens the whole mass of the coral is a danger that the coral cannot shield itself from.

There is yet another factor in the question of the repair and regeneration of corals, and it is the factor that is so intimately bound up with the problem of the limitless liability of the corals as a class to become modified and to vary. When a name is given to this factor, and it is stated that the corals are a plastic group, it is not quite easy to say what that name should rightly connote; but although the words when used in their more common sense are not at all apt, I would say that the corals are an impressionable and responsive class of animals. They are ready to comply with the demands of their environment; they are, within narrow limits, resourceful and capable of remarkable compromises between the contending forces of inherent growth-form and alterations demanded by changed surroundings.

Judged as we judge the higher animals, the corals are a class of unstable individuals: we can say definitely that a young elephant will grow up to be an elephant and no other beast; but we cannot say that an embryo Millepore will grow to be a branching *M. alcornis* and not a plate-like *M. complanata* or *M. verrucosa*; we cannot foretell that a young colony of *Pocillipora* will certainly be *P. brevicornis* and not *P. nobilis*, for, depending on the conditions of its surroundings, it might chance to be either.

This very plasticity shows itself not only within the limits of a certain species, but in the life of every actinozooid, for each member of a colony, or each solitary coral, shows in its life, its growth, and its repair, all those endless conformations to the demands of its environment that tend to produce change throughout the whole world of living things. An actinozoon, then, as an individual, possesses a birthright that gives it a maximum power of repair of damage, or regeneration of lost parts; and in the colonial forms, which are of special importance in the economy of the class, this power is greatly intensified.

In the group of solitary corals there is no very great interest attached to the processes of repair. The individual animal is at times damaged by injury, and the damage is repaired by the laying down of new calcified material, causing an irregularity in the symmetry of the animal. As a common feature of repair in any living thing, it may be noticed that the new material laid down tends to be excessive; and few large Fungiæ are to be found in which some injury has not caused the development of a quantity of irregular calcification, where the delicate tissues of the animal have been split over the sharp edge of one of the rays. Excessive injury leads to local death, and local death may affect a very large area of a solitary coral without being necessarily fatal to the whole animal. The individual has but little power of repairing a large portion of its surface when once the area is

definitely dead—very often for the reason that parasitic algae and sponges attack the dead area.

It is not till the colonial forms are reached that the power of repair possessed by the corals is properly seen. In a colony composed of myriads of individuals each actively living, each capable of growth and repair, the very best conditions for repair are at hand, and this is further aided in many cases by the peculiar mode of growth of the colony. There are some inherent characteristics of the lowly animals amongst which the corals rank zoologically that are very wonderful, and that are opposed both to the order of things that prevails in the higher classes, and also to the popular conception of the life-history of the reef-building corals.

I think it is fair to say that the average belief with regard to the building of corals and coral-reefs is that the zooids live and grow, flourish and die, and that their dead bodies form mausoleums on which their progeny found their colony, and thus build islands. Now, in contradiction to this, is the biological fact that the actinozoid is a living thing that knows no time of youthful vigour, no waxing to a period of adult life, no waning to senility—it knows no age—it practically knows no natural death. There is no building on the dead bodies of ancestors, no perpetual dying and new birth; and a colony of Madreporae will contradict this popular fallacy at one glance, for, whatever the age of the growth, the parent anthozoid flourishes till death or accident overtakes the whole. It is a wonderful thing—and one that is not, I think, generally considered—that the age of some of these individuals in every colony must be excessive, even reckoned as we reckon the age of higher animals. When we consider the very slow rate of growth of some corals, and the great size of some of the colonies to be seen every day on an atoll reef, and when we rightly understand their mode of growth, and recognise that the pioneer organism of the colony is still flourishing there, we cannot help being struck by the excessive antiquity of that organism as a living entity. That an apical zooid of a branching Madreporae colony should be ten years old seems wonderful, but these individuals are mere juveniles when some of the component zooids of massive growths are considered.

Throughout the prolonged life of these lowly animals the process of repair is a possibility, and a strange paradox is presented in some forms, for the most aged member of the colony shows the greatest activity in all the processes of renewal and repair.

The coral colony increases in size by the budding-off of new zooids and the deposition of new calcium carbonate in their tissues, and just as this is the ordinary mode of growth, so it is the ordinary mode of repair. The type of repair naturally tends to follow the type of growth of the injured colony; and the various genera of corals might be taken in order and the details of the repair of injury noted for each genus. But it is more likely that some idea of the bionomics of the group will be gathered from

the general study of the phenomena as they affect the life-history of the coral, than from a survey of the manner in which the, by no means satisfactory, classification of the types affects the phenomena.

1. *Among the colonial forms there is a sympathy of individuals, so that each member of a colony takes its share in resenting the injury to a part, and by an increased activity tends to compensate for its loss, or to assist in its repair.*

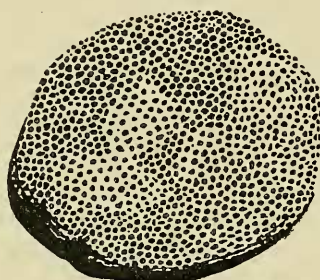
In connection with this sharing of each individual in the fortunes of its fellows and of the entire colony, it may be remembered that it was stated that the whole population of a colony may suffer shock from an injury inflicted upon only a small portion of it, and that even the zooids remote from the seat of injury will frequently not re-expand for forty-eight hours after the injury was inflicted, and this is so even when the injury is very trivial.

Now after the receipt of an injury, the effect produced by this communal sympathy varies in different forms of coral, for in a colony, as we have seen, all the members may be of equal importance, or some may be of greater value than others as producers and directors of growth.

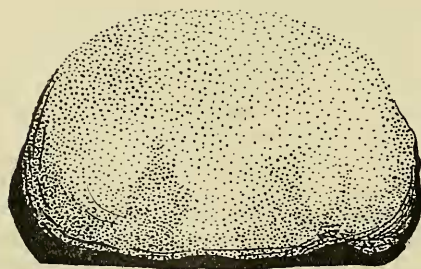
(A.) In a coral such as the massive forms of *Porites*, where the growth-tendency is to form spherical masses, every living entity in the whole vast crowd of active members bears an equal share in building and in reproducing. It is this equality of all the zooids in the community that produces the characteristic spherical form of the young growth, and the equality of the zooids plus the receipt of injury produce the typical flat-topped circular rocks into which the old colony generally shapes itself. When a mass of *Porites* has attained some size as a sphere, the zooids that lie below are necessarily stamped out of existence by the weight of the accumulated mass. It is not often, of course, that the environment is so ideal that anything like a perfect sphere is ever formed, but still, in sheltered pools, many forms of corals may be obtained resting free on the bottom, with every portion of their surfaces living. The original nucleus has been covered equally upon all sides, and the weight of the colony is not sufficient to cause the death of those zooids that happen to live on the under side. But as this mass increases in size and weight, death of the lowest zooids must inevitably occur, and the rest of the surface-area carrying on the compensating building, will cause the growth to become dome-shaped. Theoretically, the dome shape would be the type of form of all the massive species that follow this method of growth and division, but practically the dome shape is far less common than the flat-topped rock, and this is for the reason that injury to the uppermost zooids is usual in the life-history of a colony.

When the dome has become of some size, its upper surface becomes large enough and flat enough to form a resting place for sediment, and the uppermost zooids decline in activity, the compensating growth carries the sides further out, and the colony tends, by the increase of the rest of the surface, to become still more flattened at the top. Injury caused by loosened fragments sweeping over the surface of the rocks, and the further deposition of sediment, finally cause the wholesale death of the zooids of the flattened tops, and now their fellows round the margins form, by their active growth, swelling lips about the plateau, and make cushion-like bosses that tend to enclose a central flat depression in which sand accumulates, and on which other and differently growing species of coral may lodge and flourish.

Text-fig. 157.

Young *Porites* mass grown equally round a central nucleus.

Text-fig. 158.

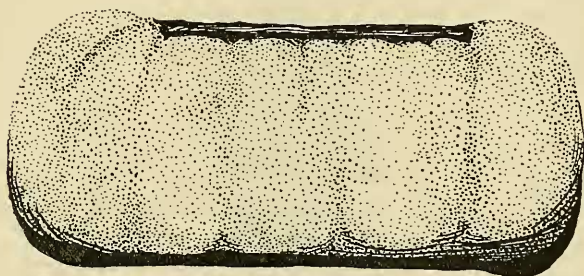
Older *Porites* colony in which the lower zooids are killed by pressure.

This process may be described as the normal accident of the life-history of those species in which the equality of the zooids of every portion of the colony is a life-condition; and it furnishes a good example of the rule of Nature's utter disregard for the life of the individual, for all those zooids on the upper surface must

certainly be killed by sedimentation or by injury, when they have succeeded in making their colony of sufficient size.

The same process that leads to the normal shaping of massive coral colonies may be seen on a small scale at myriad points upon the surface of the growth. The actual amount of living tissue in a large growing boulder is very small, for the depth to which the living animal tissues of the zooid extend beneath the surface is very slight, and yet the calcified portion that extends from the living margin to the centre of the rock must in no way be regarded as the accumulated and dead remains of past generations; for it is in reality the skeletons of those zooids whose mouths are now showing at the surface. It follows therefore, that since the skeleton devoid of animal tissues is incapable of carrying out any repairs, a superficial injury is most likely to lead to the death of a definite area of zooids on the surface—this area representing the base of a cone whose apex is at the centre of the colony (text-fig. 145, p. 521). The zooids over this area, if definitely destroyed

Text-fig. 159.



Adult colony of *Porites* in which the upper zooids are killed by sediment.

in the extent of all their living animal tissues, are not regenerated, but a sympathetic growth takes place round the edges of the area, and new material is thrown out, new zooids are budded off, and the dead area is finally invaded and covered from the active zooids of the edge. It is due to this process of repair that many of the boring molluscs become enclosed in corals, for when the surface has been attacked and killed, the margins by their sympathetic activity tend to bridge over the injured area and enclose the mollusc, which finally comes to rest in a cavity beneath the surface of the coral.

The rounded cysts found in the substance of most specimens of the massive corals, and which contain an encysted mollusc, are therefore not to be regarded as entirely the work of the mollusc, but are due to sympathetic activity of zooids in the coral colony.

Besides boring molluscs, several species of worms attack corals and hollow out tunnels this way and that through their living

substance, and here too, the sympathetic reaction of the zooids is shown. The tunnels destroy whole groups of zooids and replace the solid skeleton of the coral by a series of tubes, and the strength of the whole colony is greatly diminished; around these tubes the uninjured zooids divide and grow with increased activity, new calcium carbonate is thrown out, and an attempt is made to compensate for the destruction of tissue caused by the worm. Some curious results are brought about in this way, and specimens in which worm-boring has led to fantastic growth are always to be found, for few corals escape their inroads. A tunnel running superficially, or in the thickness of a plate-like growth, leads to an increased activity of surface-growth of the zooids, and the tunnel stands out boldly from the surface, covered and strengthened by an ever advancing layer of coral. In this way a tunnel may actually bridge a space from one plate to another, and its mouth be carried out clear of the general surface of the coral, for where the tunnel goes the surface-layer of coral ever keeps pace.

(B.) The question of the processes of repair becomes further complicated in those corals, such as the Madrepores, in which all the members of the colony are not of equal importance. We have seen, in considering the mode of growth of such corals, that the very first individual in a colony may continue to flourish and lead the growth of the entire community as long as that community lasts. The original zooid that, as an embryo, settled on the basis that formed the site of growth may be the "directive" zooid of the entire colony, and the apical zooid may represent the oldest living animal matter in the community. But besides the "directive apical zooid," others arise at intervals by budding from the sides, that are possessed of more inherent vitality than their fellows, and from their first birth they tend to grow out as new directive zooids and lead to lateral branch formation—and besides, these more virile lateral zooids are the hosts of individuals that in the normal condition of the growth reach no greater dignity than a uniform projection of their corallites.

Now when injury or destruction affects a portion of the colony, it reacts on individuals whose functioning values in the economy of the colony are not equal, and so we should expect that the result of injury or destruction would vary according to the different parts of the colony on which the maximum of damage falls. And this is the case. The actual results of repair of various injuries inflicted in experiment, or by Nature, will show more clearly the relative values and functional activities of different portions of such a colony, than will any amount of theorising or speculation.

1. If the injury be so inflicted that the branch of a Madre pore colony is broken transversely, and the injury is limited to a mere fracture of the cross section, then the repair takes place by the activity of the "apical directive zooid."

There is, as we have seen, no portion of a Madre pore colony that normally dies, and the obliteration of animal tissues in the

proximal portion of any zooid is a late change; and therefore, if the fracture takes place not very far from the end of a branch, the inherent vitality of the terminal zooid predominates, and it starts the repair by continuing to grow out in the direction of its original axis of growth, and by budding new zooids from its sides.

In a measured specimen that was fractured cleanly across one of the main branches without other injury to the colony, the apical zooid had, at the end of a hundred days, grown out 1 centimetre and had budded from its sides forty lateral daughter zooids; and the general surface of the fractured end showed seventy newly-formed coralla of old and new zooids. During the same

Text-fig. 160.



Type of repair of Madreporae when the "dominant apical zooid" is not destroyed. Process at the end of 100 days.

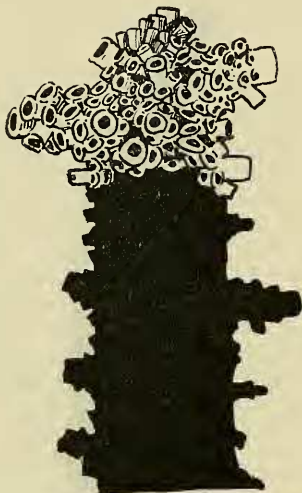
interval of time a branch of about the same diameter on the same colony, that had received no injury, had advanced by 1.5 centimetres and had added about a hundred and twenty new lateral zooids; so that, judged as growth in these corals must be judged, the rate of repair is a rapid one. In this case the dominant zooid is apical, and its superior vitality enables it to regenerate and to continue the growth along the lines of original branching; but if the vitality of the "apical directive zooid" is definitely destroyed, a very different state of affairs is brought about.

2. If the "apical directive zooid" is destroyed, and especially if the damage is extensive and affects a large area of a branch, the predominant functions of the apical zooid are taken over by the

more vigorous lateral zooids, so that there is a tendency towards branch-formation below the site of injury.

This state of things, when put into terms of the life functions of the colony, means that potentially almost any lateral bud possesses the inherent vitality of the apical zooid, but it is only in times of stress to the colony that this potential power becomes actual. A stem of a Madrepora colony may shoot up straight for the distance of a foot, and show nothing more worthy of the name of a branch than the normal projections of dominant zooids scattered irregularly over its surface; but if sufficient damage be done to it to destroy the apical zooid as well as a fair portion of its entire length, then the remaining part will at once start

Text-fig. 161.



Type of repair of Madrepores when the "dominant apical zooid" is entirely destroyed. Process at the end of 100 days.

budding with vigour. The best examples of this mode of repair are seen in those cases in which a colony is attacked by filamentous algæ. The thin green threads of this parasite enmesh the branches, and penetrating into their substance, lead rapidly and certainly to the death of the part attacked. Artificially produced injuries also provide good examples of this mode of repair. The first stage is noticed when, in contrast to the dead terminal portion, the living part swells out, its dominant zooids become more conspicuous, and their projections increase until they arrive at a stage at which they themselves give off lateral buds. The number of these enlarged lateral zooids may be very great, but not all of them ever attain the dignity of actual branch formation.

By the end of a hundred days after the receipt of injury the uninjured central end of a branch is roughened all over its surface by the projections of lateral zooids, and those of them that will form new branches have already begun to develop secondary buds from their sides. This process cannot be spoken of with absolute accuracy as an actual repair, for the part injured surely dies, and its substance is never regenerated; but it is a process by which the sympathetic activity of the remaining zooids in the community is called into action, and the potential power of branch formation inherently lodged in the dominant lateral zooids is turned into a real power. The value of this process in the life-saving of a species is obvious, for the growth tendency of a Madrepore colony is to steadily develop upwards, and the limit of this upward growth is either at the water-level, or at a level at which protection from rough water and moving fragments afforded by the shelter of surrounding rocks, is lost. Now a colony that grows up beyond its upward limit of safety will sooner or later have its terminal ramifications killed by exposure, or broken by waves or moving fragments; and the injury that destroys the power of the apical zooid causes the lateral buds to branch out at angles to the parent stem, and spread fresh zooid-bearing surfaces far and wide in the area of safety. It is this process that is the great determining cause of the general growth tendency of Madrepore colonies, and the one that causes the deep-water and shallow-water forms of the same species to vary in their vegetative forms of growth.

3. If in a colony the injury is such that the apical zooid is neither injured nor destroyed, but the damage is limited to the surfaces of a branch, then the repair takes place as in colonies in which every zooid is of equal value.

This repair is well seen after experimentally inflicted injuries, and the process of carrying out the regeneration of the destroyed area is very like that previously described as occurring in those corals that grow like the massive forms of *Porites*.

The first step is the active marginal growth and the formation of an excessive quantity of new material, which, in the form experimented on (*Madrepora pulchra*), is at first of a light-blue colour, and is semi-transparent. In this new material the mouths of corallites soon appear, and the edges become covered by a host of uniform zooids, which soon spread over the entire area destroyed by the injury, provided that the area is not too large, and that no alga settles on it in the meanwhile. It may be stated here that in experimental injury, many experiments fail for the reason that the destroyed or injured area commonly becomes a focus for the invasion of boring parasites, worms, molluscs, sponges, and algae, and the pure results of injury and repair become complicated.

Where no such complication existed, areas of 5 by 5 millimetres, 20 by 8 mm., 20 by 10 mm., and 25 by 12 mm., were completely covered by new material with a multitude of new zooids in the

course of 100 days, whilst larger areas were commonly attacked by sponges or algæ before repair was completed. Very much the same process is seen to occur when constricting metal bands are placed round branches. The zooids, where the bands exert their pressure, are destroyed, and the general growth of the branch and the sympathetic activity of the zooids at the margin of the injury soon tend to cause the band to sink into the substance of the coral, and to become completely embedded beneath the surface.

It was previously stated that the type of repair naturally tends to follow the type of growth of the injured colony; and this is generally true. If a coral has a particular mode of growth, and if it be in such an environment that its mode of growth is the one most suitable, then an injury is repaired or a part regenerated on the same type of growth as that of the colony. But the particular form in which a colony may be growing may not be the form best suited for successfully flourishing in that particular environment; and then, following an injury, a remarkable state of things is brought about, which may be stated as follows:—

II. *A coral may repair an injury by a new growth of a different type to that of the colony, and in such cases the repair growth is of a form better suited to the environment than is the form of the parent colony.*

It must be borne in mind that the physical conditions of the atoll are not absolutely constant; seasonal changes in sets and strength of currents are perpetually causing alterations at all points of the island ring, and a habitat may alter greatly in its physical conditions in the course of a few months. When a coral embryo settles down upon a basis, and starts the founding of a colony, the type of growth that will result will be what is best fitted to the environment as the embryo finds it. But suppose that, after the founding and growth of a colony, the physical conditions of the environment change, rough water is admitted, silt settles down, or the water becomes shallow and calm: then the growth of the colony may not be the ideal one for flourishing under these new conditions.

In many places where the conditions are prone to vary, the habitat of the corals may alter in its physical nature in more or less regular cycles. Where, as at the eastern extremity of Pulu Tikus, a spit runs out, building sheltered pools and protecting the shore for a considerable distance, and then later on, in the periodical cycle of currents and eddies, is carried away; many corals must be subjected to a great variation of environment. In such circumstances no doubt many colonies die, for, as we have seen, a sudden change of habitat cannot be resisted when a form is well adapted for one definite kind of environment, and in any case the colonies are liable to injury and partial death in their changed surroundings.

When such injury falls on a coral not ideally situated, the

repairing growth exhibits a strange independence, and, forsaking the growth-form of the colony, builds its repair in the form best suited to the new conditions of the environment.

This is a strange zoological fact, that the inherent growth-form, once stamped upon a well-established colony, continues to be the type of growth, though it be but ill adapted to its habitat; and yet, when the continuity is once broken and a new start is made, the newly-budded zooids can throw off the stereotyped method, and build anew to the altered conditions.

It is facts such as these that give some clue to the understanding of the vast range of variation occurring within the limits of a species, and make the establishing of a species a matter of extreme doubt, until every possible variation that different surroundings will stamp upon the type has been examined. We have seen, in following the life-history of corals, that the colony shows great adaptability, being able to mould its growth in response to the demands of its environment, and in this repair process it possesses a further power, for it can entirely alter the structure of an established colony.

Numerous examples of this strange process may be seen. A branching Montipore, growing in a gap in the island ring, is found to have every colony dead or damaged in a greater or less extent of its whole growth. The damage is probably due to the fact that currents have altered the physical conditions of the habitat since the founding of the colonies, and that a greater rush of water has brought more sand and moving particles in contact with them, for the apical branches of all the colonies within a definite area will be found broken. The repair of this damage invariably takes the form of an amorphous encrusting growth covering the debris of the dying colony, the regenerated portion keeping pace with the destruction, and thus keeping the colony living—but living as an entirely different type of its species. (Pl. XXIX. fig. 1.)

Madrepore colonies show the same phenomena, and very strange repair-forms of *Pocillopora* growing in rough water as encrusting growths may be found.

When, after repair, a Madrepore colony assumes an encrusting form, as it frequently does, the inherent tendency of its growth is still evident, for rising at intervals from its flat surface are numerous dominant zooids, which, were the opportunity afforded them, would form upward-growing branches.

It is by no means uncommon, in this process of repair, not only for the vegetative growth of the colony to be altered, but for the actual type of the corallum to be changed. When a Montipore repairs its own ill-situated and dying colony by an encrusting growth, the whole minute structure of the coral is changed. Instead of the smooth surface over which the fairly wide mouths of the corallites are dotted, is a coral with an outward appearance notable chiefly for its extreme roughness, due to the development of numerous papillæ at the bases of which open the minute

corallites (Pl. XXIX. fig. 1). The characters of the original growth and of the repair growth are so entirely different, that they would certainly be regarded as two distinct species. Other examples of this entire change are not uncommon, and some very strange abnormalities may be found, which show that in repair, as in adversity and in alteration of environment, there is practically no limit to the developing of the different main types of growth by any coral. It is common in repair of injury as it is in cases of adversity, that the bounding walls of the newly-budded zooids are never completed, and repair by a pseudo-meandrine form of fission is often met with in many and widely-separated species of coral (Pl. XXIX. fig. 2). It is common, too, to find that the repair-zooids have raised coralla, when those of the parent colony are flat, and in these cases it is probably silt that has caused the original damage.

The study of the repair in corals is therefore one not devoid of zoological interest, for it shows clearly that a type must never be considered as a species, in the way in which we regard species among the higher animals, until it has been seen in all its variations, and until all the possible modifications that repair produces have been studied.

That a type like the encrusting Montipore should be in reality the same species as the branching form, would be considered as highly improbable, but when it is seen that the one type repairs its damage by the development of a new growth of the other type, there is no alternative but to regard them as identical species.

That the numerous types of *Millepora* and of *Pocillopora* should be but variants of a single species would seem at first sight to be very unlikely, for there is little enough likeness between the extreme forms, and yet their processes of repair show them capable of building to any of their diverse types, regardless of the nature of the parent growth.

If the processes that have been described, and the conclusions that have been drawn from them, be accepted, they can serve only to make clearer the great fact that morphology—the animal's type—is the outcome of necessity; and here the demands of necessity bring about change, not in the life-history of a species only, but in the life of the individual.

Since these repair-forms are the outcome of the partial death of the colony, and since the growth-forms of many colonies are determined by the normal, or abnormal, death of portions of their surface, it will be well to briefly review the processes by which death overtakes a colony.

The subject of repair leads naturally to the consideration of the death of the organism, for when the destructive processes outweigh the resources of repair, then death must inevitably ensue.

There is one fact in the life-history of corals that the study of their processes of repair clearly brings out, and it is this, that all

the methods of regeneration are more for the life saving of the colony than of the individual. It is a rule with Nature that the life of the individual is a thing of little moment: Nature has little care for individuals, though she strives always to maintain the life of the species. In a vast community of individuals, as is a coral colony, each separate member is but a part of the whole body, and the preservation of the colony is a thing of more import than the saving of a few individuals. A branching Madrepore grows naturally upwards into the danger zone, and the terminal branches are inevitably destroyed, with the sacrifice of a myriad of zooids; but the result is a stimulus to lateral branching within the area of safety, and the colony continues to flourish.

In every massive growth starting to develop on all sides of a nucleus, those zooids that are budded below can never hope to live, and those on the upper surface will in all probability die. In all the processes of repair that have been described, it is not the individual that is mended, for an individual once badly damaged is not repaired; but the loss is made good by the growth of new zooids that take on the functions of those lost. Repair in colonial forms does not save the individual from death, but it preserves the life of the colony. Now loss by death in a colony is not always repaired.

We have seen that the flat tops of the massive growths of *Porites* remain devoid of living zooids, and in several types of growth, death of a portion of the colony is more or less usual; among the branching *Porites* it is normal to find the lower portions of the growth dead, and no attempt made at their repair.

When it is said that the partial death of a colony is more or less usual in some types of growth, it is not in any way meant that the progress of coral formation is a building of the living zooids upon the dead bodies of past generations, for the partial death is due, as a rule, to very definite outside causes.

In this atoll the greatest cause of coral death has been a quite unusual one, but it has been a most instructive one, for it brings out some very interesting facts in the life-history of corals. In 1876 all the living coral of the south-east portion of the lagoon was entirely destroyed, by the pouring out of foul water from a volcanic vent at the southern side of the atoll. The picture presented by these denuded areas was described by Dr. H. O. Forbes in 1879, and by Dr. Guppy in 1888; and in 1906 there is still the same tract of dead coral on which the efforts at re-colonisation have been practically unavailing.

This remarkable failure of the corals to repopulate a large portion of the lagoon, is probably due to the fact that during the period immediately following the disaster, various algæ such as agar-agar and several other species, being of a faster and more hardy growth, stepped in and took possession of the area before the slow growing corals could obtain a proper footing. The growth of algæ is in itself hostile to the life of corals, and,

apart from that, the algæ beds in the lagoon are the greatest factors in catching silt, and piling up the shifting sand-banks the presence of which is so fatal to coral-growth. These two factors, aided perhaps by subsequent minor volcanic poisonings, have so completely paralysed all coral activity, that to the south of Pulu Selima there has been in many places no trace of new growth; and the abnormal death that occurred thirty years ago has to this day remained unrepaired.

Although such events as this are quite exceptional in the life-history of corals, or of coral islands, still the after history of the disaster shows on a large scale the influences of those factors that in the normal life of corals tend to bring about their death. It is the silt and seaweed that have prevented corals from flourishing on their old site, and the silt and seaweed are to-day in the atoll the two great causes of coral death.

The influence of matter suspended in the water is one of the most far-reaching factors in the life-history of corals: it is to resist its effects that many of the vegetative forms are evolved; it is on account of the silt that many acres of the lagoon are devoid of coral-growth; and it is probably on account of the presence of silt that wave action is so necessary to coral life, and that the unstirred depths below about 20 fathoms are comparatively bare of coral.

Silt, sand, or suspended matter may cause the actual death of corals in two ways:—(a) It may fall upon them and choke their zooids from above. (b) It may overtake them from below.

Of these two actions examples are always to be seen in (a) the partial death of the tops of massive *Porites* colonies (text-fig. 159, p. 541, & Pl. XXIX. fig. 2), and in (b) the stems and lower branches of branching *Madrepores* which are normally lifeless. In these cases the death is only partial, for the reason that the colony is one capable of resisting as a whole the amount of suspended matter normally present in the waters of its habitat; but if the amount be suddenly increased, then the colony may be unable to resist it, and general death ensues. Evidences of this mode of death are seen in the gaps in the island ring where an alteration of current brings more silt than is usual to the growing colonies, and very interesting results may be produced experimentally. On December 13th, 1905, several healthy living colonies of rough-water forms of *Madrepora* and *Pocillopora* were removed, without exposure or injury, from their habitat of rough barrier water, and without any delay were placed in marked sites in a sheltered sandy pool of the barrier-flats. In the same pool, which is almost completely cut off from the sea at low tides, and then contains about 2-3 feet of water, and which is about 100 yards long by 20 wide, numerous corals live and flourish, calm-water forms of *Madrepora* and *Pocillopora*, capable of resisting silt, being the most abundant. The